

Placoderm (Pisces: Placodermi) Remains from Lower Devonian Rocks at Taemas, New South Wales

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This paper describes six new specimens of placoderm fish from the Early Devonian limestone sequence of Taemas in southeast New South Wales. All these specimens contribute to our understanding of the morphology of taxa at this time of early evolution of the group. They include: a paranuchal plate of *Errolosteus* which suggests a sliding neck joint for this genus; an incomplete head shield of a brachythoracid including the left and right central, right preorbital, postorbital and marginal plates with a portion of the endocranium attached showing a dorsal ossification; two specimens of *Arenipiscis*, an incomplete head shield including left and right centrals, anterior of nuchal, left and right paranuchals, right preorbital, postorbital and marginal and a small piece of the left preorbital plate, with the second specimen a nuchal plate with a complete posterior margin; a brachythoracid with a more extensive right marginal plate than previously known and an incomplete postorbital plate; and a brachythoracid skull with palate and endocranial ossification showing a unique parasphenoid, a new condition for the pituitary vein on the palate, a double hyomandibular articulation, a previously undescribed myodome in the orbital cavity, a distinctive buccohypophysial foramen, anterior supragnathals and a dorsal articulation on the autopalatine of the palatoquadrate.

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INTRODUCTION

Some Early Devonian limestones in southeast Australia contain a rich fauna of placoderm fish. The placoderm remains discussed in this paper were collected by Prof. K.S.W. Campbell and C.S. Findlay of the Geology Department, Australian National University (ANU), and Dr G.C. Young of the Australian Geological Survey Organisation (AGSO). The material was found in the Warroo and Crinoidal limestones of the Taemas Formation (Fig. 1), approximately 12 kilometres south of Yass in southern New South Wales. Five of the specimens were found on the north shore of Warroo Creek at the junction with Burrinjuck Dam, Yass Sheet 1:100 000, grid reference 8628-667303. The seventh specimen, ANU 49125, was found on the shore of Burrinjuck Dam, Yass Sheet 1:100 000, grid reference 8628-654319.

To avoid confusion about stratigraphic nomenclature, I have used the term Taemas Formation, and I refer to constituent units recognised by Browne and subsequent workers by an informal nomenclature that uses lower case descriptive names, eg. Currajong limestone.

The stratigraphy of this and the nearby Wee Jasper area has been described by Browne (1959) and Pedder, Jackson and Philip (1970). The Warroo limestone has a rich marine invertebrate fauna including ostracods, nautiloids, brachiopods, bivalves, gastropods and rugose corals. It has been interpreted as a quiet marine deposit formed below

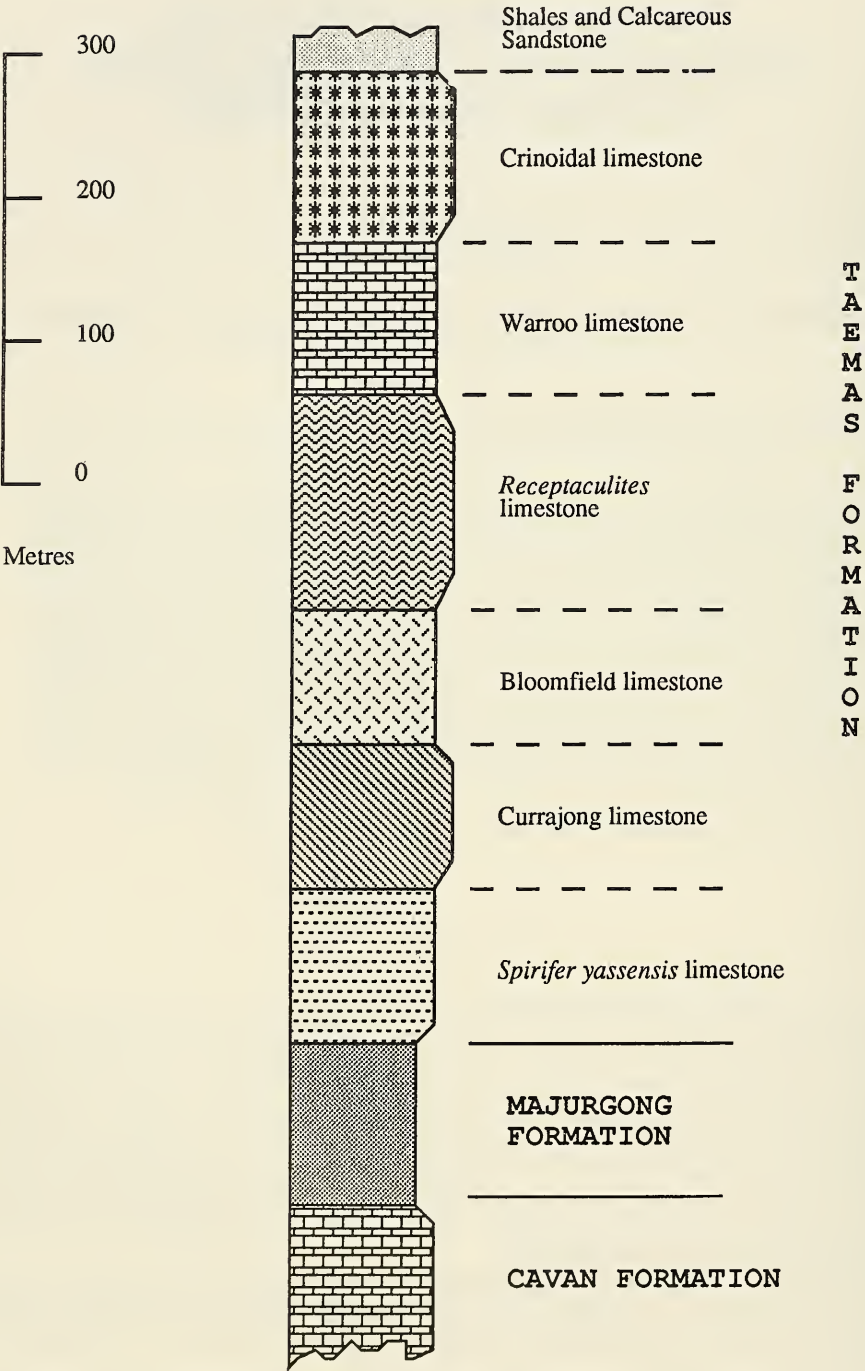


Fig. 1. Stratigraphic column of the Murrumbidgee Group showing the subdivisions of the Taemas Formation overlying the Majurgong and Cavan Formation.

wave base. The overlying Crinoidal limestone is considered to have been deposited on a more shallow marine bank which was periodically covered with crinoids.

The dating of these two units presents a problem because they have as yet yielded no conodonts or other zonal fossils of value for inter-regional correlation. However, conodonts have been described from the western outcrop at Wee Jasper by Pedder et. al., and it is possible to use local fossil assemblages to make a correlation between the Taemas and the Wee Jasper sequences. The basal two units, the Cavan and the Majurgong Formations can be recognised in both areas. Within the overlying Taemas Formation previous workers have recognised the *Spirifer yassensis*, Currajong, Bloomfield and *Receptaculites* limestones. However, the Warroo and Crinoidal limestones are unique to the Taemas area. In the western outcrop at Wee Jasper, the post-*Receptaculites* rocks consist of massive limestones containing many mound-like constructions. It is presently assumed that these represent facies equivalents of the Warroo and Crinoidal limestones.

The currently accepted international division of the Lower Devonian into Stages and their associated conodont zones are shown in Figure 2 which is part of a figure prepared by Oliver and Chulpác (1991), Mawson et. al. (1992) have provisionally placed the Pragian-

SERIES	STAGE		CONDONT ZONE
	W. EUROPEAN	BOHEMIAN	
LOWER DEVONIAN	EMSIAN	DALEJAN	<i>P. cost. patulus</i>
			<i>P. serotinus</i>
		ZLICHOVIAN	<i>P. inversus</i>
			<i>P. gronbergi</i>
			<i>P. dehiscens</i>
	SIEGENIAN	PRAGIAN	<i>P. pireneae</i>
			<i>Eogn. s. kindlei</i>
			<i>Eogn. sulcatus</i>
	GEDINNIAN	LOCHKOVIAN	<i>Ped. pesavis</i>
			<i>Anc. delta</i>
			<i>O. eurekaensis</i>
			<i>I. w. woschmidtii</i>

Fig. 2. Subdivision of the Lower Devonian based on Oliver and Chulpác (1991) and Ziegler (1979).

CATALOGUE NO.	LOCATION	HORIZON	DESCRIPTION
CPC 31618	Warroo Creek	Crinoidal lst.	left paranuchal plate <i>cf. Errolosteus goodradigbeensis</i>
CPC 31619	Warroo Creek	Crinoidal lst.	skull roof <i>cf. Parabuchanosteus murrumbidgeensis</i>
CPC 31620	Burrinjuck Dam	Warroo lst.	skull roof Gen. indet. sp. indet.
CPC 31621	Burrinjuck Dam	Warroo lst.	nuchal plate <i>cf. Arenipiscis westolli</i>
CPC 31622	Burrinjuck Dam	Warroo lst.	marginal and postorbital plates Gen. indet. sp. indet.
ANU 49215	Burrinjuck Dam	Crinoidal lst.	skull roof <i>cf. Arenipiscis westolli</i>

Fig. 3. Specimens described in this paper.

Emsian boundary at the first appearance of *P. dehiscens dehiscens* in the Cavan Formation. The *dehiscens* Zone is known from the Cavan Formation in both the Taemas and the Wee Jasper areas (Philip et. al. 1967). The Taemas Formation therefore is unequivocally younger than basal Emsian. Pedder et. al. recognised *Polygnathus linguiformis foveolatus* from ca. 230 metres above the base up to the top of the Taemas Formation at Wee Jasper. Klapper and Johnson (1975) assigned this subspecies to *P. perbonus*, whose appearance ushers in Mawson's *perbonus* Zone. This zone is correlated with the *gronbergi* Zone overseas (Klapper and Johnson 1980). The appearance of this form occurs well below the *Receptaculites* limestone equivalents. The Warroo and Crinoidal limestones cannot therefore be older than the *gronbergi* Zone. The upper limit can be fixed according to Mawson (1987) by the occurrence near the top of the Taemas Formation of some members of the group assigned to *Polygnathus linguiformis linguiformis* by Pedder et. al. (1970, Plate 40, Figs 6 & 8). These Mawson considers to belong to 'delta morphotype' of *Polygnathus serotinus*, characteristic of the *serotinus* Zone.

Consequently, the post-*Receptaculites* units must lie between the upper part of the *gronbergi* Zone and the *serotinus* Zone. In terms of the Bohemian sequence, this means they cross the Zlichovian-Dalejian boundary. Zeigler (1979) considered these zones to cross from the early to the late Emsian.

The six placoderm specimens which are listed below (Fig. 3) add to the information given in previous studies. This paper deals only with new information and subsequent reinterpretation of previous descriptions where applicable.

The preparation of the material was carried out using acetic acid of 5% or 10% strength to dissolve the limestone matrix, depending upon the strength of the bone (Toombs 1948). The exposed bone was strengthened with polyvinyl butyral (sold under the trade name Mowital) diluted with alcohol.

Five of the specimens collected and described for this paper are registered with the Australian Geological Survey Organisation, within the Commonwealth Palaeontological Collection and have the prefix 'CPC'. Associated material referred to from the same source has the same prefix. One specimen has the prefix ANU and is located in the Geology Department of the Australian National University. Another specimen referred to, from the Australian Museum, Sydney, has the prefix AMF.

The stratigraphy of the Crinoidal limestone was originally described by Browne (1959). It is now considered (Findlay 1991) to have been deposited on a carbonate platform at the base of which there are channels which have yielded rich placoderm material. Above the Crinoidal limestone are interbedded shales and calcareous sandstone formed in a somewhat different environment. They will be the subject of a subsequent paper by the author.

SYSTEMATIC DESCRIPTIONS

Order EUARTHRODIRA Gross 1932

Suborder INCERTAE SEDIS

Infraorder INCERTAE SEDIS

Genus ERROLOSTEUS Young 1981

Type Species: Errolosteus goodradigbeensis Young 1981, from the Taemas Formation, Emsian.

Remarks

CPC 31618 has been compared with the genus *Errolosteus* on the basis of the dermal ornamentation of parallel ridges with tubercles on them as described for the holotype. The allocation of *Errolosteus* to the Infraorder Brachythoraci Gross 1932 assumes that the genus has a ball-and-socket neck joint consisting of thick bone. The neck joint for the type species is unknown. Specimen CPC 31618 suggests a sliding neck joint and shows a unique pattern for the overlap areas of the paranuchal, nuchal and central plates. Long (1984) assigned an anterior dorsolateral plate with a short rounded condyle from the Buchan fauna to this genus on the basis of surface ornamentation of "...concentric ridges bearing small tubercles" (Long 1984, p. 178), and the compatible shape of the plate with the dorsal margin of the anterior lateral plate of *Errolosteus* described by Young (1981). However, the pattern of these parallel ridges on the Buchan specimen does not show the longitudinal direction of the rows which diverge at sharp angles between groups of ridges across single plates, as can be seen on the holotype and CPC 31618. The dorsal margin of the anterior lateral plate of *Errolosteus* (Young 1981) is not preserved, preventing comparison with the Buchan specimen. As CPC 31618 is a topotype, it is possible Long's material from Buchan may belong to a different genus. The identification of this genus on the parallel ornamentation alone should be approached with caution.

cf. *Errolosteus goodradigbeensis* Young 1981

Figs 4, 5

Material

CPC 31618, an almost complete left paranuchal plate.

Horizon

Warroo limestone.

Discussion

The dermal ornamentation is comparable with the description given for the holotype. Both specimens show parallel ridges with tubercles of approximately the same spacing on the paranuchal plates. The distinctive pattern of ridges meeting at sharp angles on single plates can be clearly seen on CPC 31618 (Fig. 4A, 5A) and the holotype.

The posterior section of this bone is very thin for a paranuchal. Normally this plate in a brachythoracid has a thickening of the bone at its posterior end to incorporate the ball-and-socket joint of the neck. The possibility that CPC 31618 was weathered has been considered and rejected because such weathering would have had to be intense and localised at the point of the joint. However, the small notch at the posterior of the plate where the sensory groove passes off the plate shows no sign of weathering and the posterior margin is complete. This, coupled with the absence of thickening, suggests the neck joint was a sliding one.

Compared with *Taemasosteus* White (1952) and *Parabuchanosteus* White and Toombs (1972), the overlap areas of this paranuchal plate are distinctive. As is normal, the nuchal plate overlaps the paranuchal, but is overlapped by an unusual protuberance forming a notch (*no*, Fig. 4A) on the paranuchal. A similar notch pattern has been found between different plates on *Buchanosteus confertituberculatus*, where the marginal plate carries a notch onto the central plate (Young 1979, Fig. 1). This notch on the marginal and central plates is also found on a placoderm specimen described by Lelièvre (1989, Fig. 2). These are the only other occurrences of this feature in Early Devonian arthrodires known to me.

Suborder PHLYCTAENIOIDEI Miles 1973

Remarks

The higher classification for the following specimens is based on that proposed by Young (1979). This system is applied by other authors (eg. Long 1984) for the fauna from southeastern Australia. Alternative classification systems have been proposed eg. Denison 1978.

Infraorder BRACHYTHORACI Gross 1932

Family BUCHANOSTEIDAE White 1952

Genus PARABUCHANOSTEUS White and Toombs 1972

Type species

Buchanosteus murrumbidgeensis White 1952, from the Taemas Formation, Emsian.

Remarks

This specimen has been allocated to the buchanosteid group as the surface ornamentation of tubercles, the pattern of the skull roof plates and the lateral line pattern represent the general pattern found in that group. The parasphenoid of CPC 31619 most closely resembles that described for *Parabuchanosteus*.

Parabuchanosteus was differentiated by White and Toombs (1972) from *Buchanosteus* by the different shapes of the parasphenoids. That bone in *Parabuchanosteus* is described as "...spade-shaped...as wide as long...largest medially in front and crossed towards rear with a deep groove...pierced by a pair of foramina in centre". Young (1979) disputed this and concluded that *Parabuchanosteus* is a junior synonym of *Buchanosteus*. He proposed an allometric growth pattern for the parasphenoid based on the examination of three new specimens, ANU 21805, 21818 and 21807, from the Taemas fauna, and comparison with previously described material, and attempted to show that *B. confertituberculatus* fell within the allometric growth range. In my opinion the bones of the three new specimens do not "...provide evidence that parasphenoid shape varied with size" (Young 1979) as they are not attached to specimens that allow an unequivocal identification of genus or species. Therefore, though the argument may be valid, it requires support from more complete material. Further, the three specimens from Taemas referred to by Young (1979) are not topotypes and it has not been established that the species in the two locations are identical in other characters; hence, in view of the fact that the three new parasphenoids in question are not associated with other skeletal material that can be compared with the types of *Buchanosteus*, they must be interpreted with caution. The new specimen described here, CPC 31619, has a parasphenoid that most closely resembles that of the type of *Parabuchanosteus* figured by White and Toombs (1972, Fig. 5). Meanwhile it is noted that the new material has a myodome within the orbit which is not found in previously described buchanosteid material. Although Young (1979) has described myodomes within the orbital cavity of species he has described as *B. confertituberculatus* (Chapman), this specimen, CPC 31619, shows a myodome of different shape, size and position. This may be grounds for further consideration of the validity of two genera.

CPC 31619 agrees with the general pattern of sensory canals and plate boundaries described in previous literature for buchanosteids, in particular the description given by Young (1979). A number of new features previously undescribed contribute to a better understanding of the buchanosteid group. These include a different parasphenoid shape, anterior supragnathals, articulation facets on the dorsal and ventral surface of the endocranium, a different pattern for the pituitary vein on the palate, and a large myodome within the orbital cavity.

cf. *Parabuchanosteus murrumbidgeensis* White and Toombs 1972

Figs 6, 7, 8, 9

Material

CPC 31619, an incomplete skull roof including the palate, parasphenoid and endocranium.

Horizon

Crinoidal limestone.

Discussion

Skull roof

This specimen is represented by two pieces. These have been kept separate to facilitate analysis of the endocranium but are restored in Fig. 6A to show the pattern of the

lateral line canals. The smaller piece has most of the lateral line canal pattern which indicates the extent of the skull roof and the individual plates. The large piece has a considerable amount of endocranium attached.

The posterior pitline on this specimen is long and continuous forming a deep channel. This has not been described previously for buchanoosteids. The taxonomic significance of continuity of the lateral line canal system is not well understood. However, it is worth noting that Ørvig (1971) illustrated different lateral line patterns in arthrodires with varying degrees of representation of the posterior pitline. Each genus has a distinctive position or degree of representation for the posterior pitline. There does not appear to be significant variability within a genus.

The indentation half way down the infraorbital sensory canal (*ioc*, Fig. 6A) is interpreted as a post-depositional artefact.

Parasphenoid

The parasphenoid on this specimen most closely resembles the description given for *Parabuchanosteus*. Its left side has been slightly distorted and compressed in a medial direction with a deep groove containing a single buccohypophysial foramen. Previous workers described the buccohypophysial foramina as paired (White and Toombs 1972) or bilobed (Young 1979, Hills 1936). This suggests that the opening may be variable on the ventral surface of the bone and the actual division may take place within the bone. Central to the posterior half of the parasphenoid is a deep, regular cruciform furrow, previously undescribed. The denticles associated with this furrow are larger and more pointed than those on the rest of the parasphenoid, and are orientated towards the centre of the furrow.

External surface of endocranium

The anterior section of the endocranium is visible in dorsal view as a bilobed convex structure in an anterolateral position to the parasphenoid. This area on CPC 31619 (Fig. 6A) has been displaced in a lateral direction and, as this area is poorly known in primitive arthrodires, it is difficult to determine how much of the endocranium has been displaced. This entire bilobed structure is not endocranial, as on its ventral surface there is ornamentation interpreted as denticles. The area covered in denticles appears to be a separate bone and is interpreted as a pair of anterior supragnathals (ASG, Fig. 6B). Like advanced arthrodires, primitive arthrodires have been assumed to have had two pairs of supragnathals, a posterior pair associated with the autopalatine section of the palatoquadrate, and a previously unknown anterior pair, lying in an anterolateral position on the ethmoid region of the endocranium. If the above interpretation is correct, this will be the first known occurrence of anterior supragnathals in a primitive arthrodire.

Articulation facets, *art*₁ and *art*₂ (Fig. 6A) identified on the dorsal and ventral surface of the endocranium are considered to be the counterparts to the articular facets found on the palatoquadrate, as described for *Buchanosteus confertituberculatus* (Young 1979, Fig. 15). A third articulation surface, *art*₃, can be seen on this specimen (Fig. 6B), but does not correspond with the *art*₃ of Young (1979).

No groove or canal for the pituitary vein (i.e. the subpituitary fenestra) on the ventral surface of the endocranium, such as is normal for buchanoosteids, has been observed on this specimen. There is a series of foramina in approximately the correct position (*f. pv*, Fig. 6B) where blood vessels from the roof of the mouth could have drained into the pituitary vein which must have been located internally to the palate.

The anterior postorbital process has an open end which is divided into two by a strut of dermal bone, with the more posterior one being triangular and the anterior one oval (*apo*, Fig. 6B). White and Toombs (1972) noted that the end of the anterior postorbital process is always unossified and presumably bore a cartilaginous area for articulation of the hyomandibular. This specimen suggests a double articulation on the hyomandibular (*art. hm*, Fig. 8), previously unknown.

The hyomandibular nerve foramen is clearly shown adjacent to the two hyomandibular articulations (*VII hm*, Fig. 8). The foramen found exiting the palate in a position posterior to the hyomandibular foramen (*IX*, Fig. 6B) has not been described previously in the buchanosteid group. When viewed from the posterior end of the specimen, a canal with ossified walls is seen running from this foramen into the endocranium above the palate. It is interpreted as the glossopharyngeal nerve canal.

Endocranial cavity

A previously undescribed myodome, not present on *Buchanosteus confertituberculatus* Young (1979), can be seen within the right orbital cavity above the opening for the jugular vein on CPC 31619 (*my*, Fig. 6B). Myodome structures do not normally vary significantly within placoderm species, particularly in the orbital cavity; this suggests CPC 31619 belongs to a different species from *Buchanosteus confertituberculatus*. The separate ossification of the jugular canal and the facialis canal found on CPC 31619 is in contrast to the description given for *Buchanosteus confertituberculatus* by Young (1979), where the two vessels are described as having occupied a single ossified canal, again suggesting a specific difference.

Perichondrial ossification associated with the Nerve VIII complex can be seen to run up to the skull roof (*cn*, Fig. 8) directly under the central sensory canal. This appears to be a canal in cross-section which suggests the lateral line system may, in part, be innervated by Nerve VIII.

Family INCERTAE SEDIS

Genus and Species INCERTAE SEDIS

Remarks

This material has been allocated to the brachythoracid group because the surface ornamentation, position of the roof plates and associated lateral line canals follow the standard pattern found in the following three representatives of that group: *Buchanosteus confertituberculatus* Chapman 1916, *Parabuchanosteus murrumbidgeensis* White and Toombs 1972, and *Taemasosteus novaustrocambricus* White 1952. It is described here as it shows an ossified dorsal roof to the endocranium, previously unknown in this group.

Gen. indet. sp. indet.

Figs 10, 11

Material

CPC 31620, a portion of skull roof which includes incomplete left and right central plates, and incomplete right preorbital, postorbital and marginal plates.

Horizon

Warroo limestone.

Discussion

The ossified braincase is partly preserved on this specimen. The shape and location of the perichondrial ossification directly under the junction of the lateral line canals on the central plate suggest part of the inner ear system which has this position in other forms (Miles 1971, Young 1979). The large lateral tube (*sem. c*, Fig. 10B) is interpreted

as the horizontal semicircular canal joined to the anterior ampulla. The anterior ampulla is connected to a larger structure interpreted as the sacculus which has been displaced. The adjacent perichondrial ossification is interpreted as the roof of the brain cavity (*r. cv*, Fig. 10B). There is no previous record of an ossified dorsal roof to the endocranium in placoderms. However, CPC 31619 described elsewhere in this paper, shows the same thin ossification.

Ossified canal walls are apparent on the ventral surface of the skull (*c. oss*, Fig. 10B), and appear to be incorporated into the endocranium, suggesting a new interpretation for the ossified canals incorporated with the ventral surface of the skull roof. This canal system has been referred to by Ørvig (1957, p. 307) as "...surely vascular, forming a wide-spread plexus, the *subcutaneous vascular plexus*...". These canals are very similar to those described by Campbell and Barwick (1982) for *Chirodipterus australis*, a Late Devonian lungfish, and *Dipnorhynchus kiandrensis*, a lungfish from the Early Devonian at Kiandra, N.S.W. These two lungfish show ossified canal walls between the dermal roofing bones and the endocranium which Campbell and Barwick have interpreted as part of the sensory system. Similar structures occur in *Eusthenopteron foordi* (Jarvik 1942) from the Upper Devonian in Canada. The concentration of these canals around the inner ear complex in the specimen under description, may indicate a relationship with the acoustic nerve which would be consistent with the view that the lateral line canals are in part innervated by this nerve.

Family INCERTAE SEDIS

Genus ARENIPISCIS Young 1981

Type species

Arenipiscis westolli Young 1981, from the Taemas Formation, Emsian.

Remarks

This genus was erected by Young (1981) on a number of criteria including the following which can be seen on the new material: fine dermal ornamentation, elongated skull roof, trapezoidal nuchal with a distinctive median ventral depression.

CPC 31621 is more complete than previously described nuchal plates (Long 1984, Young 1981) and differs in the dimensions of the plate, the central depression area and the ventral foramina. The dorsal surface of ANU 49215 differs from that of the holotype in that it shows a more extensive lateral line system and well defined sutures between plates.

ANU 49215 has been slightly distorted causing minor buckling at the anterior end of the central plates and minor separation of the plates. It is considered that the right pre-orbital, postorbital and marginal are not distorted, apart from being displaced in a ventral direction from the central plates.

The only other possible generic assignment of this material would be to *Burrinjuosteus asymmetricus* White 1978, which shows a number of similarities including the anterior shape of the nuchal plate; the shape and position of the paranuchals; the sinuous line and direction of the suture between the two centrals where the base runs from the right side of the nuchal plate to the left of the central line at the top; the anterior shape of the central plate; the possible asymmetrical shape of the centrals; ridges of thickened bone on the ventral surface; and very fine surface ornamentation. However, the proportions of the head shield, microscopic features of the dermal surface and the structures on the ventral surface more closely resemble *Arenipiscis*.

cf. *Arenipiscis westolli* Young 1981

Figs 12, 13, 14, 15, 16

Material

CPC 31621, a nuchal plate; ANU 49215, skull roof plates including left and right central plates, right preorbital, postorbital, marginal, anterior of left and right paranuchals and nuchal, and small piece of left preorbital.

Horizon

Warroo limestone (CPC 31621); Crinoidal limestone (ANU 49215)

Discussion

CPC 31621 is almost complete with only a small section of the posterior margin and left edge broken (Figs 12, 13). This permits an interpretation of the posterior margin, which is different from that reconstructed from the incomplete holotype and paratype (CPC 16972) by Young (1981, Fig. 5). The thickening of the nuchal on the ventral surface along the posterior margin is well preserved, resulting in a straight posterior margin with no apparent embayment. The posterolateral corner of the nuchal plate is more complete on CPC 31621 than on previously described material and shows this to be much broader than the thin tapering corners described for the holotype and paratype.

The foramina for the nutritive vessels associated with the median depression described for the holotype differ from those found on CPC 31621 which shows one large foramen at the posterior end of the depression, and a few smaller ones at the anterior end of the plate adjacent to the overlap areas. The central depression (*m. dep*, Fig. 12B) also differs considerably from previous descriptions. There is no "elevated crest of bone" (Young 1981) delineating the depression. Only the posterior end is well defined where it sinks into the ventral surface, rather than being raised as previously described. The anterior end of the depression is not defined on CPC 31621.

The dorsal surface shows an indentation on the right side (?*scar*, Fig. 12A), which x-radiographs show to be a surficial mark. This has been interpreted as a wound, possibly a tooth mark, as it does not resemble boring of an invertebrate.

The sutures between the plates are well defined on ANU 49215 (Figs 14, 15) and differ from those of the holotype (Young 1981, Fig. 5) in a number of ways. The anterior edges of the paranuchal plates terminate posterior to the anterior end of the nuchal plate, which in turn differs from the holotype in its width and shape at the anterior end. The right postorbital plate is complete and does not show an elongated posterior margin as suggested for the incomplete bone on the holotype. The suture between the central plates is well defined on both the dorsal and ventral surfaces. The posterior pitline and the middle pitline, clearly seen on this specimen, are not present on previously described material.

The fine dermal ornamentation found on ANU 49215 (and the holotype) has not been described before. Figure 16 shows it to be unique, differing from that illustrated for *Burrinjucosteus asymmetricus* (White 1978, Plate VII). The individual tubercles do not show the standard pattern of small domes with surrounding rosette structures; rather, they are pinnacle-like. In places the tubercles form parallel rows, with some sections of the skull roof showing pits at the base between the tubercles and other sections showing areas of tubercles orientated in one direction. Although the data are too sparse to allow a firm interpretation, this linear orientation of the tubercles and the arrangement of the pits suggest the possibility that they had some sensory function.

The ventral surface of ANU 49215 shows the same ridges (*cr. so*, Fig. 14B) as those described for the holotype, but unlike the latter they do not follow the lateral line canal. The ridge running in a rostrocaudal direction is much larger than on the holotype and has a prominent bulbous swelling, whereas the adjoining ridge (also larger) runs in a mesial direction and then curves gently in a posterior direction. The latter ridge is so oriented that it leaves a deep depression posterior to the so-called supraorbital crista (Young 1981, Fig. 6). The supraorbital crista is not directed ventrolaterally as described for the holotype, but rather is vertical.

The thickening on the ventral surface of the holotype, said to be for the semicircular canal, is not apparent on ANU 49215 (Fig. 14B), which shows a circular structure with a lateral projection to the centre on the right central plate in the same position. The remnants of a similar structure can be seen on the left central plate in the same position. From a functional perspective, it is difficult to imagine the inner ear projecting up into the dermal skull roof as suggested by Young (1981). This structure is more likely to have been a brace for the endocranium against the skull (also proposed by Young).

At the posterior end of the central plates towards the midline on the ventral surface, directly beneath the junction of the three lateral lines on the dorsal surface, ANU 49215 clearly shows a network of grooves in the surface of the dermal bone (*cn*, Fig. 14B). Branches of this network run in a posterior direction to lie under the boundary of the nuchal and paranuchal plates. One branch can be seen to run in a continuous line in an anterior direction and curve to the lateral margin along the crest of the arcuate ridge described above. Where these canals terminate, and in some cases at their junctions, pits run into the dermal roof. These canals are interpreted as part of the sensory system.

The groove illustrated by Young (1981, Fig. 6) as carrying the vagus nerve, is not evident on the holotype. In vertebrates this large visceral nerve exits the posterior portion of the brain behind the inner ear complex and always runs in a ventral direction. In fish, small branches supply the gills and taste sensation, with the main trunk running backward to the visceral region (Romer 1962). The description for the holotype would have the vagus nerve with an improbable orientation posterolaterally and dorsal into the ventral surface of the dermal roof bone. Further, it is considered the distance between the postulated vagus nerve and the position of the postulated labyrinth cavity as illustrated by Young (1981, Fig. 6), is not sufficient to allow room for the otic complex.

Gen. indet. sp. indet. Figs 17, 18

Material

CPC 31622, an almost complete right marginal and an incomplete right postorbital plate.

Horizon

Warroo limestone.

Remarks

These two plates are referred to the brachythoracid group as the surface ornamentation closely resembles the pattern found on *Parabuchanosteus murrumbidgeensis*, *Buchanosteus confertituberculatus* and *Taemasosteus novaustrocambricus*.

The only known postmarginal plates from the Taemas-Wee Jasper fauna are figured for *Buchanosteus confertituberculatus* (Young 1979, Plate 1D) a poorly preserved plate,

and for *Parabuchanosteus murrumbidgeensis* (White and Toombs 1972, Plate 1, Plate 2, Fig. 3, Plate 4) two incomplete postmarginal plates. Therefore, relationships between the marginal and the postmarginal plates are not well known in the brachythoracid group.

Discussion

The posterior section of the lateral line canal, the postmarginal canal (*pmc*, Fig. 17A), is as long as the anterior section, previously undescribed. This can be interpreted as either a long marginal plate, or part of the postmarginal plate attached. The ventral side of the marginal plate clearly shows an overlap area at the posterior end for the postmarginal plate (*oPM*, Fig. 17 B), indicating a long and narrow marginal plate ending in a point. This differs from previously described marginal plates in the brachythoracid group.

SUMMARY

The information given in this paper is useful for the further understanding of the placoderm fauna from the Taemas-Wee Jasper area. Several previously unknown features have been suggested: a double hyomandibular articulation on the anterior postorbital process of a brachythoracid; a dorsal articulation on the autopalatine section of the palatoquadrate in the same group; and, possible anterior supragrathals. The two specimens of *Arenipiscis* sp. differ from the previously described material and may represent a new species.

After comparison with specimens held within the Commonwealth Palaeontological Collection at the Australian Geological Survey Organisation, and those in the literature, it was determined that on the basis of ornamentation alone accurate identification of genera within the brachythoracid group is not possible for the Taemas-Wee Jasper fauna. A possible exception to this could be *Errolosteus* (if this is in fact a brachythoracid). Tubercles vary in density and size from plate to plate on the same individual. It is clear that individual specimens show considerable variation from almost smooth to highly tuberculate on different parts of the dermal plates. By some authors the smoothness has been attributed to wear in some instances but I consider that it may be variation between individuals of the same species, or within the genus.

In this work difficulty has been encountered in allocating specimens to species and genera because the current knowledge of the limits of the described taxa is inadequate. As a result, several specimens have been referred to as *Incertae Sedis*. This situation is exacerbated by the attempts of previous workers to assign new material from different areas to already defined taxa, without knowing the range of variation in such taxa at the type localities. It would not be surprising if, when larger topotypic collections are available, the ranges of variation of these early placoderm species were found to be wider than at present appreciated. Until this is done the contribution of the Taemas-Wee Jasper material to the understanding of the higher classification of placoderms is in question.

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TABLE 1

List of abbreviations used in Figs. 4–18.

III	nervus oculomotorius III
Vpf	nervus profundus V
VI	nervus abducens VI
VII	nervus facialis VII
VII hm	hyomandibular branch of facial nerve
VII pal	palatine branch of facial nerve
VIII	nervus acusticus VIII
IX	nervus glossopharyngeus IX
ASG	anterior supragnathal
a. amp	anterior ampulla
a. orb	orbital artery
apo	anterior postorbital process of endocranium
art _{1–3}	articulation facets
art. hm	articular facets for hyomandibular
b. lat	nervus buccalis lateralis
C	central plate
cn	canal
c. oss	ossified canals
cr. so	supraorbital crista
csc	central sensory canal
d. end	external opening of endolymphatic duct
d. endi	internal opening of endolymphatic duct
f. bhy	buccohypophysial foramen
fla	flange
f. pv	foramina associated with pituitary gland
if. pt	infranuchal pit
if. r	infranuchal ridge
ioc	infraorbital sensory canal
M	marginal plate
m. dep	median depression
ml	median line
mlc	main lateral line sensory canal
mp	middle pitline
my	myodome
Nu	nuchal plate
no	notch
oC	area overlapping or overlapped by central plate
oM	area overlapping marginal plate
oNu	area overlapped by nuchal plate
oPM	area overlapping postmarginal plate
oPNu	area overlapping or overlapped by paranuchal plate
oPtO	area overlapping postorbital plate
oSO	area overlapped by suborbital plate
orb	orbit
PNu	paranuchal plate
PrO	preorbital plate
Psp	parasphenoid
PtO	postorbital plate
plp. C	posterior process of central plate
pmc	postmarginal sensory groove
pp	posterior pitline
r. cv	perichondral roof of cranial cavity
reV	trigeminus recess
sac	sacculus
sem. c	semicircular canal
soc	supraorbital sensory canal
v. pit	pituitary vein

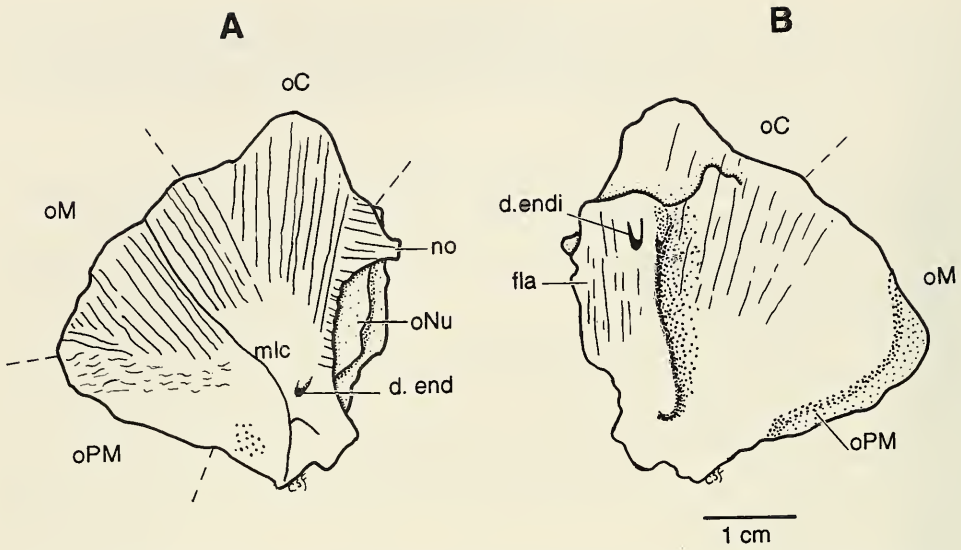


Fig. 4. cf. *Errolosteus goodradigbeensis*. Drawings of left paranuchal plate, CPC 31618. A, dorsal view; B, ventral view.

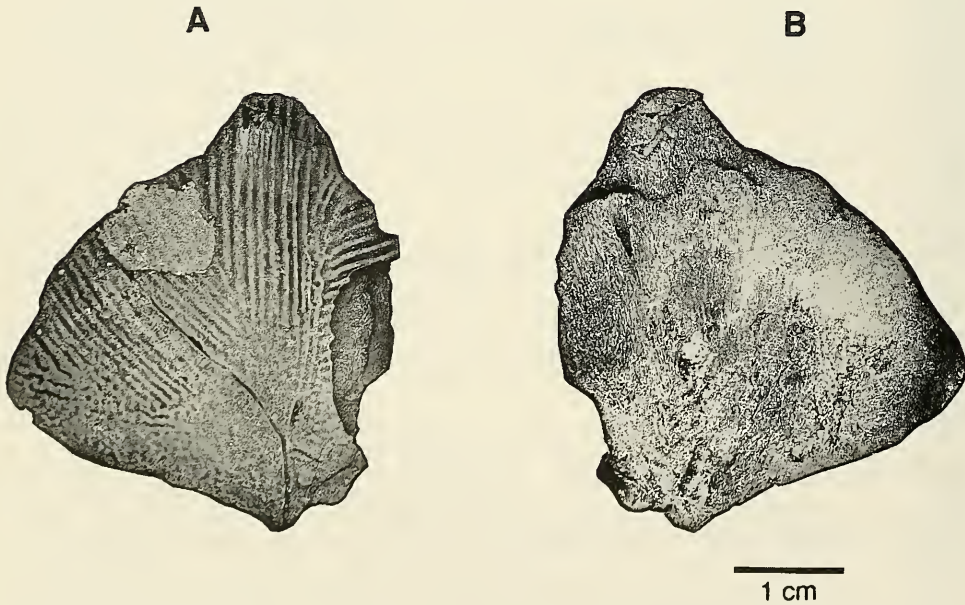


Fig. 5. cf. *Errolosteus goodradigbeensis*. Left paranuchal plate, CPC 31618. A, dorsal view; B, ventral view.

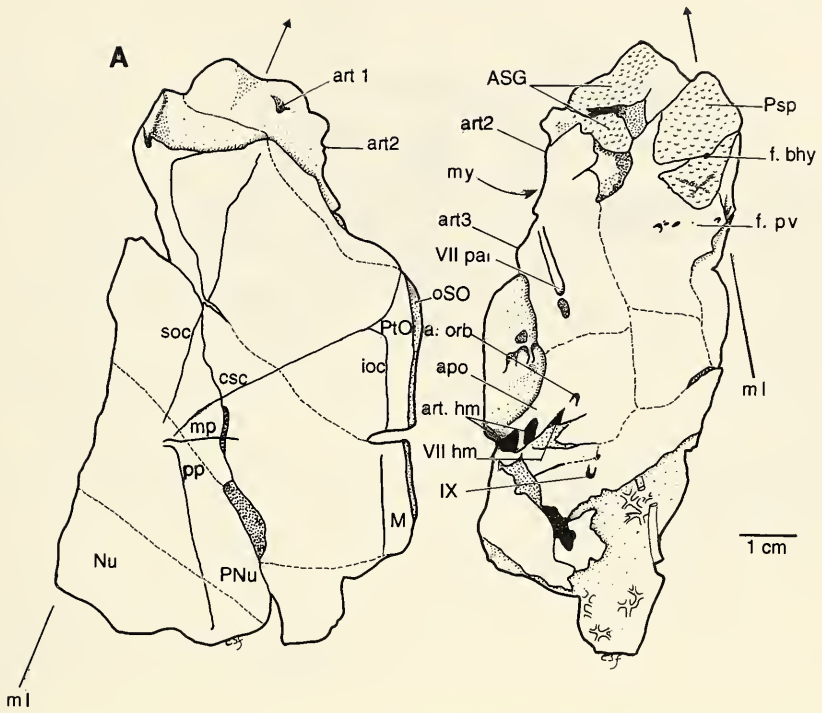


Fig. 6. cf. *Parabuchanosteus murrumbidgeensis*. Drawings of portion of skull, CPC 31619. A, dorsal view with both pieces together; B, ventral view of larger piece.

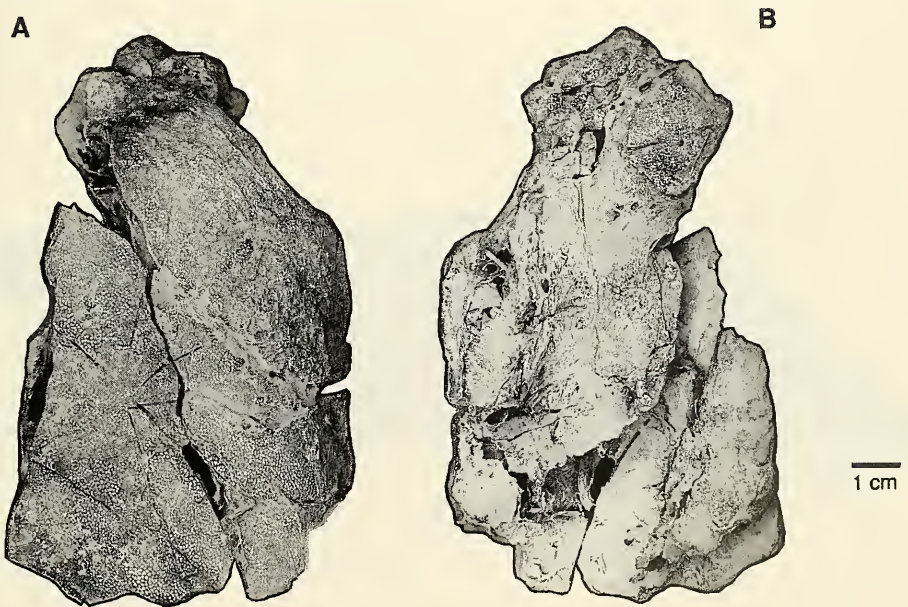


Fig. 7. cf. *Parabuchanosteus murrumbidgeensis*. Portion of skull, CPC 31619. A, dorsal view with both pieces together; B, ventral view of larger piece.

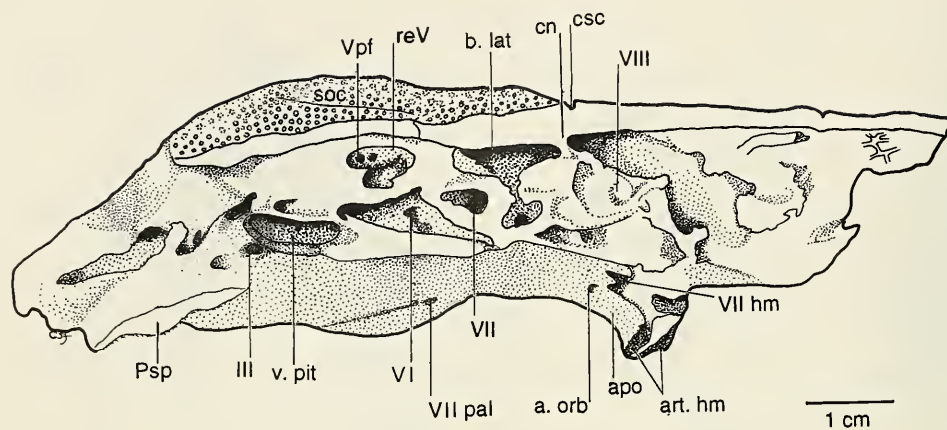


Fig. 8. cf. *Parabuchanosteus murrumbidgeensis*. Drawing of portion of skull, CPC 31619. Medial view of larger piece showing internal features.



Fig. 9. cf. *Parabuchanosteus murrumbidgeensis*. Portion of skull, CPC 31619. Medial view of larger piece showing internal features.

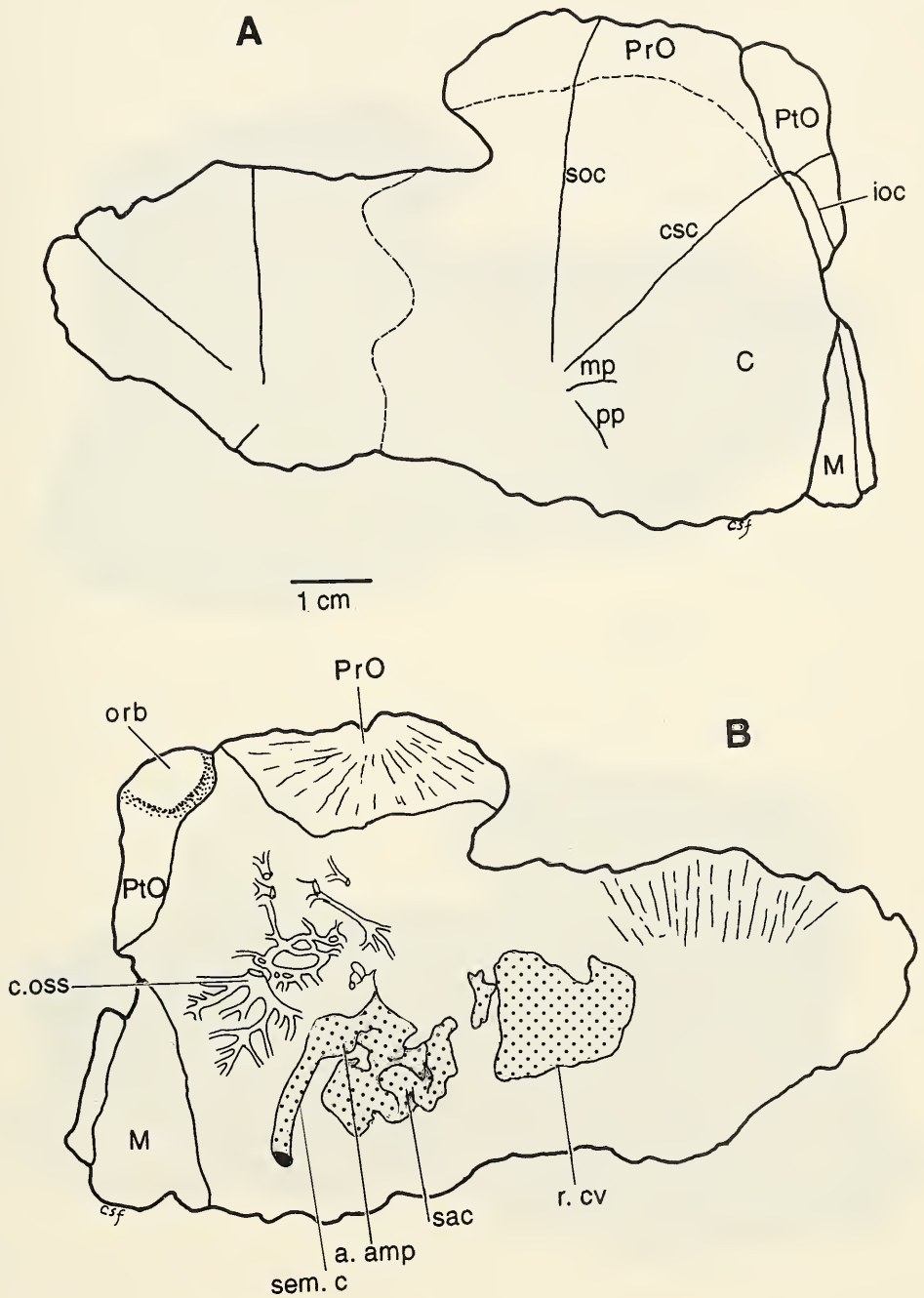


Fig. 10. Gen. indet. sp. indet. Drawings of portion of skull roof, CPC 31620. A, dorsal view; B, ventral view.

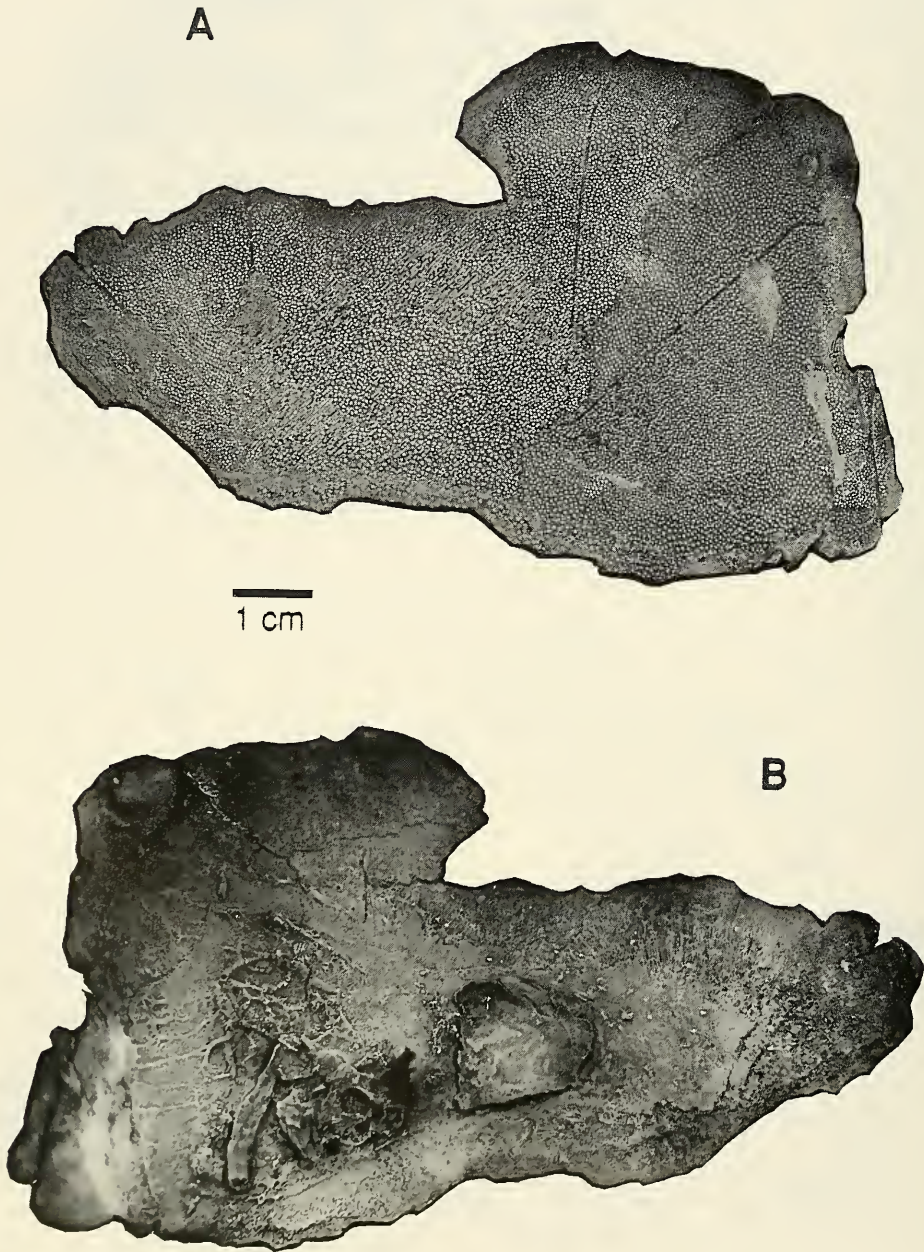


Fig. 11. Gen. indet. sp. indet. Portion of skull roof, CPC 31620. **A**, dorsal view; **B**, ventral view.

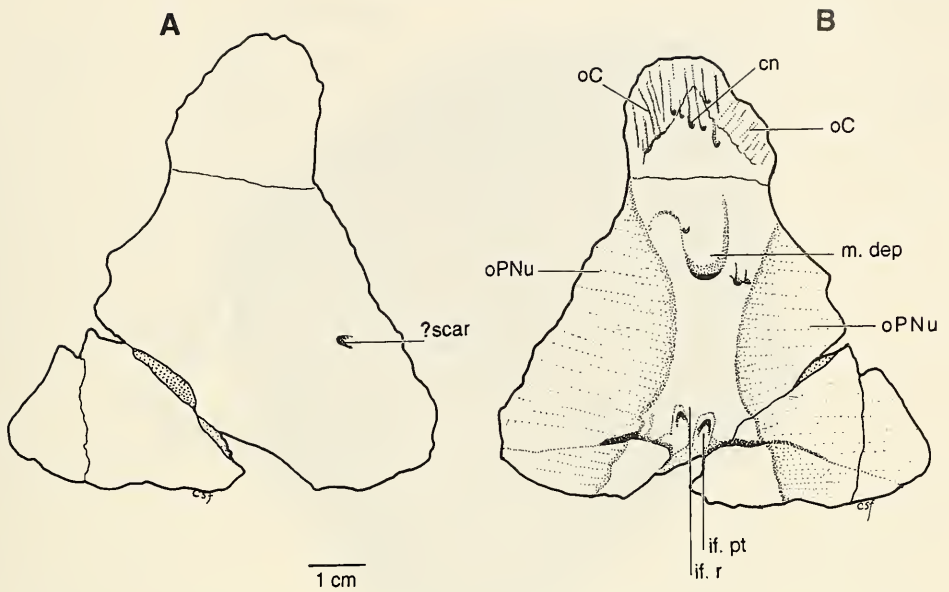


Fig. 12. cf. *Arenipiscis westolli*. Drawings of nuchal plate, CPC 31621. A, dorsal view; B, ventral view.

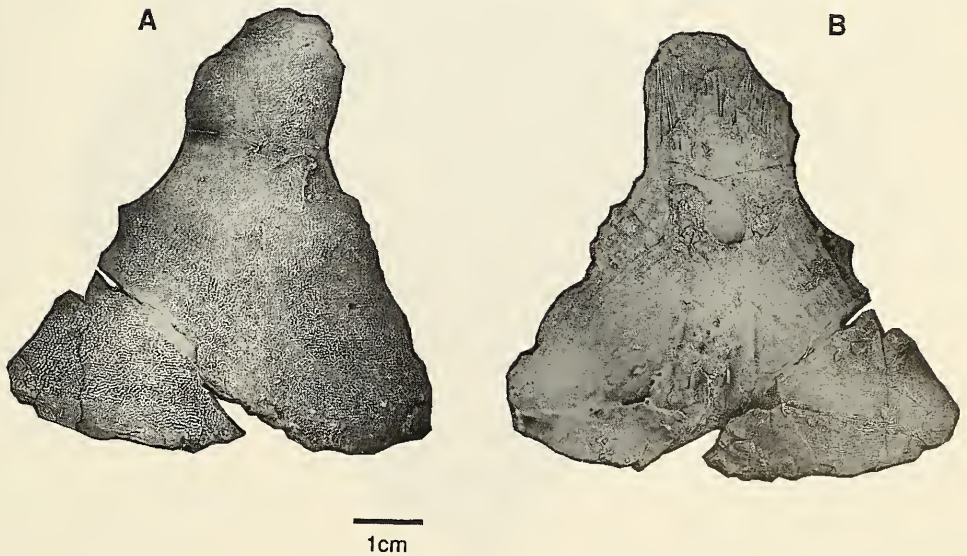


Fig. 13. cf. *Arenipiscis westolli*. Nuchal plate, CPC 31621. A, dorsal view; B, ventral view.

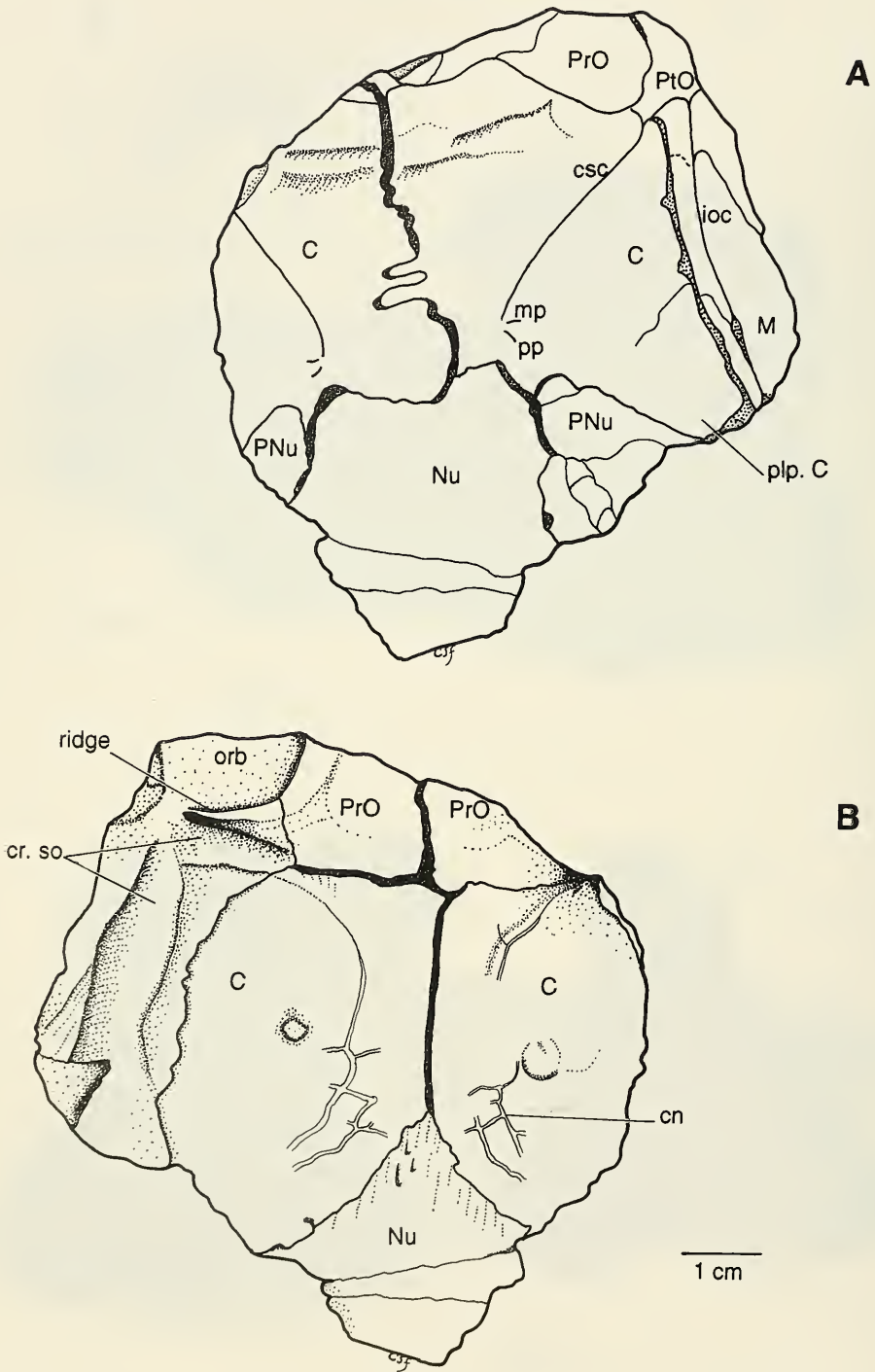


Fig. 14. cf. *Arenipiscis westolli*. Drawings of portion of skull, ANU 49215. A, dorsal view; B, ventral view.

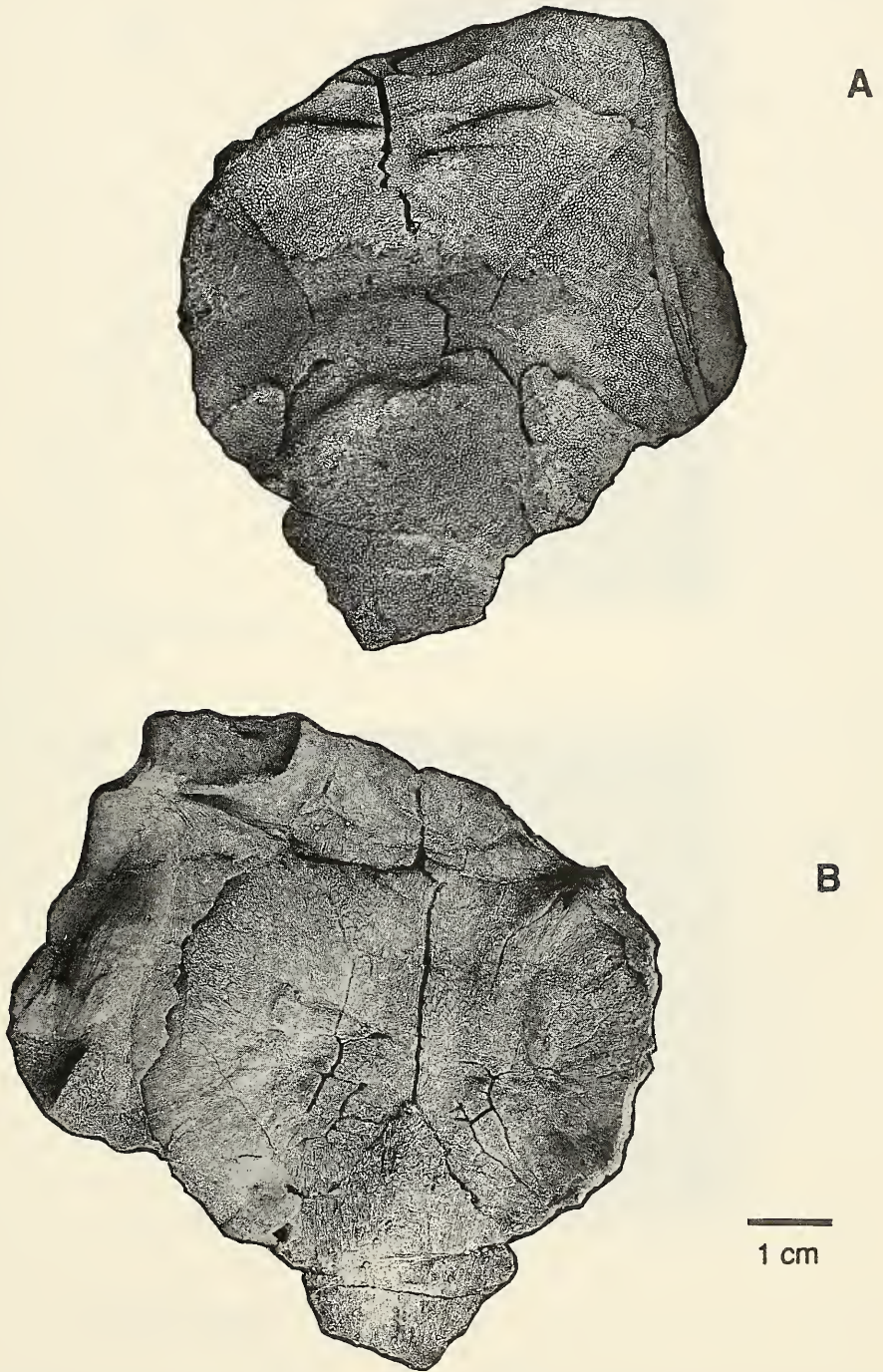


Fig. 15. cf. *Arenipiscis westolli*. Portion of skull, ANU 49215. A, dorsal view; B, ventral view.

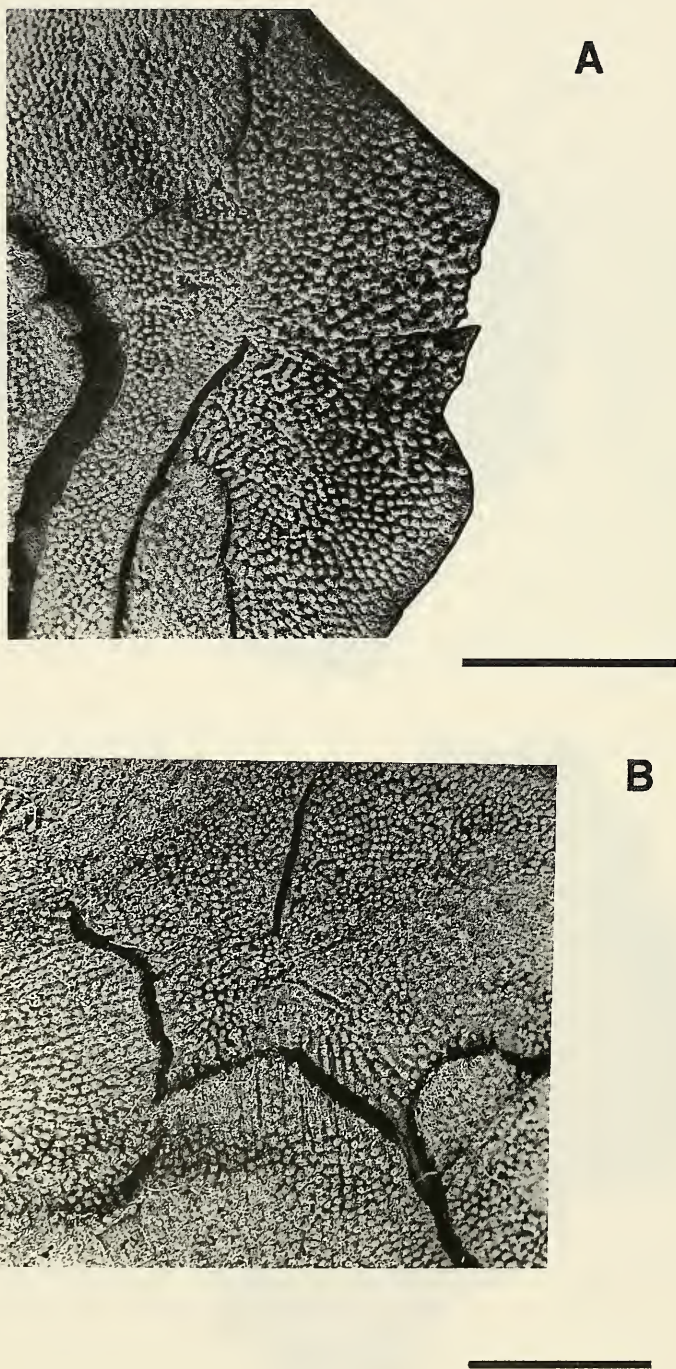


Fig. 16. cf. Arenipiscis westolli, ANU 49215. (A) Junction of central, marginal and postorbital plates showing the structure of the tubercles and (B) Junction of nuchal, central and paranuchal plates showing the linear pattern of tubercles. Scale bar represents 5mm.

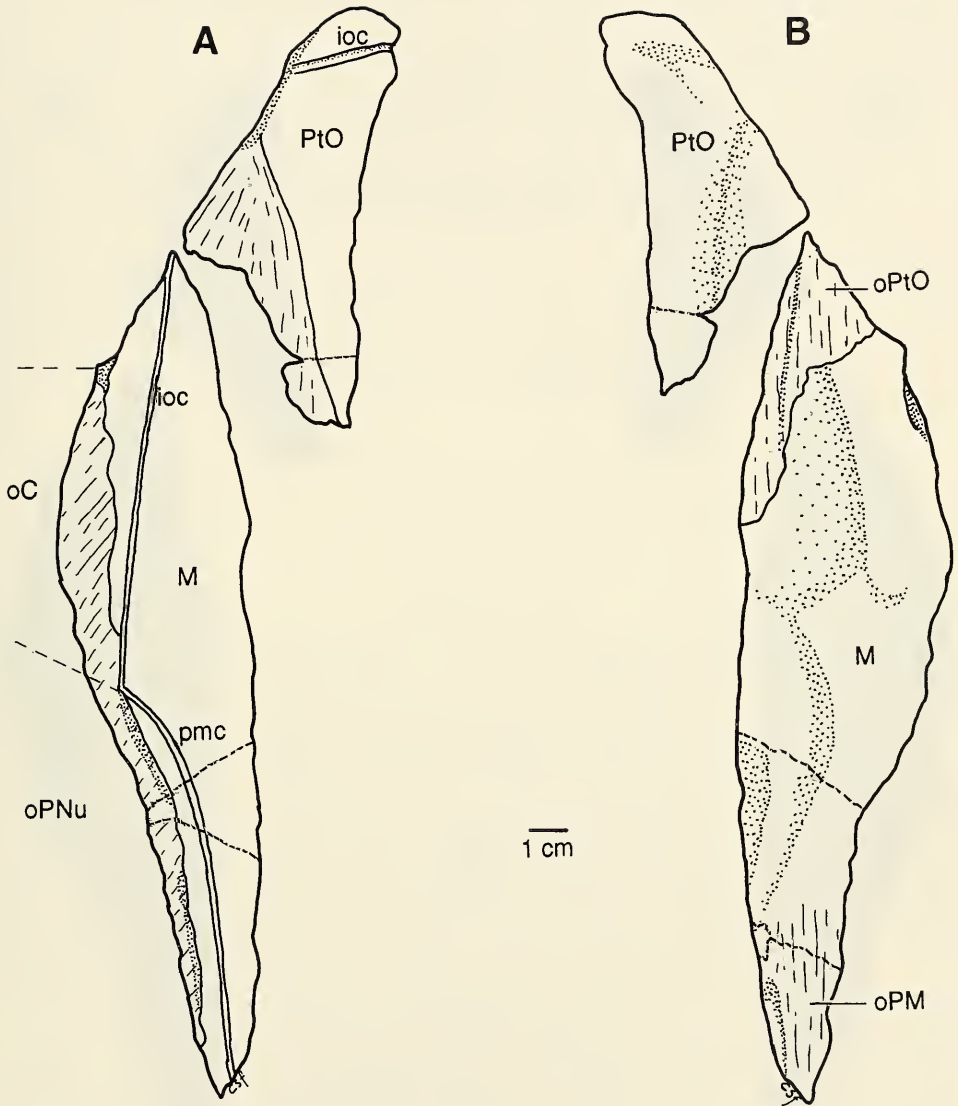


Fig. 17. Gen. indet. sp. indet. Drawings of incomplete right postorbital and marginal plates from the skull, CPC 31622. A, dorsal view; B ventral view.

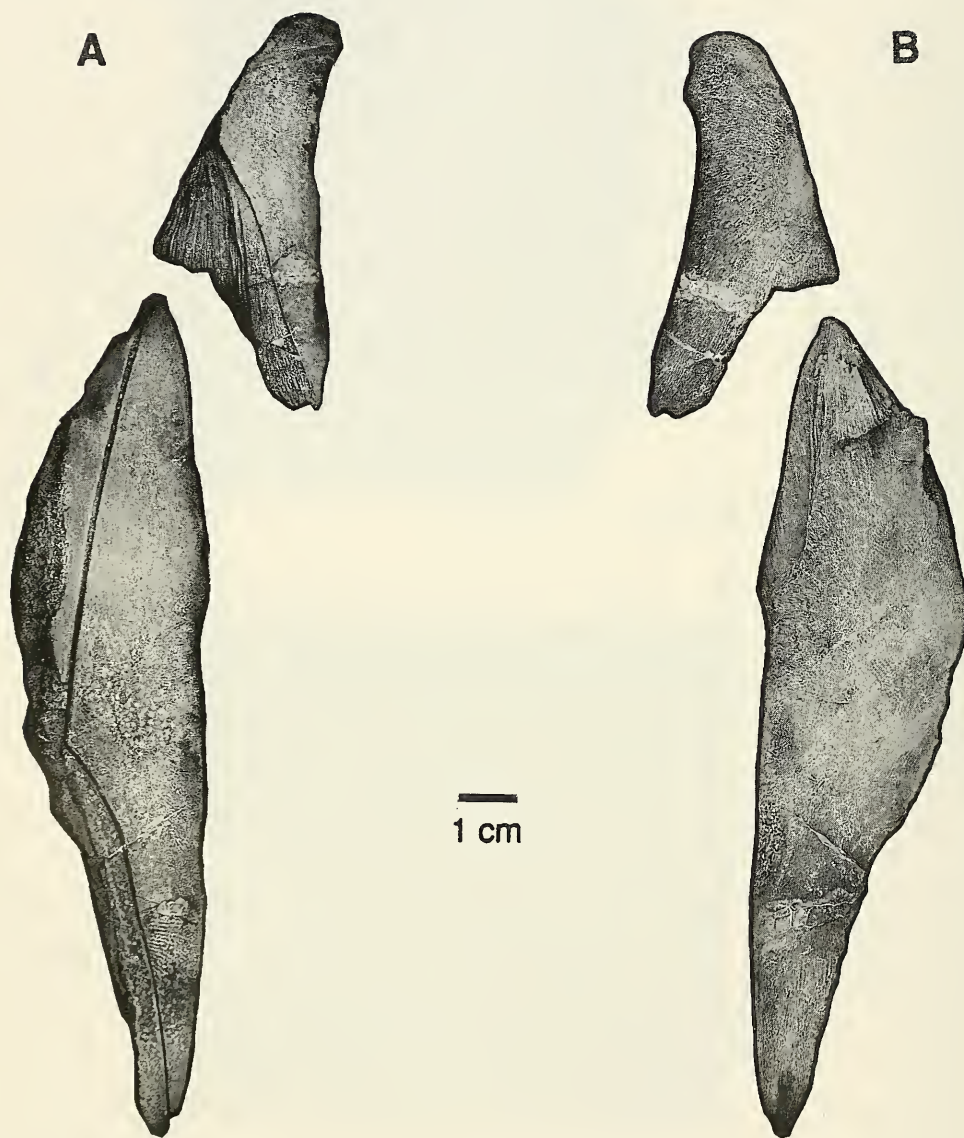


Fig. 18. Gen. indet. sp. indet. Incomplete right postorbital and marginal plates from the skull, CPC 31622. **A**, dorsal view; **B** ventral view.